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Antennal Responses to Hydrodynamic and Tactile Stimuli in the Spiny Lobster *Panulirus argus*

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Abstract. The responses of the long, spiny, antennal flagella of the spiny lobster *Panulirus argus* to hydrodynamic and tactile stimuli were investigated. Experiments were performed in the dark and included videographic laboratory studies of small tethered lobsters (<20 mm carapace length) and nighttime field observations of larger, subadult, foraging animals. The antennae are held laterally in both tethered and free-ranging animals. Water jets trigger bilateral antennal responses in which both flagella are swept forward for rostrally directed stimuli, backward for caudal stimuli, and in an intermediate backward direction when stimulated laterally. Mean response angles are greater for caudal stimuli (17°–48°) than for rostral stimuli (10°–16°), and lobsters exhibit lateralized sensitivity when jets are directed from the caudal sector, as indicated by larger ipsilateral responses—up to twice the amplitude of contralateral responses in field experiments. Untethered lobsters frequently turn the body in the direction of the water jet and tailflip away or tailflip without first turning. Tactile stimuli to the lateral edges of the antenna, carapace, walking leg, abdomen, and tailfan also trigger primarily backward sweeps of the antennae. Only the antennule and medial antennal receptive fields yield forward movements, and these elicit smaller responses (mean response ≤ 5°) than in the backward direction (mean responses up to 15°). Threshold tactile stimuli trigger exclusively ipsilateral responses; thus, lateralization is absolute. These results demonstrate that spiny lobsters accurately localize mechanosensory stimuli and direct their antennal flagella in the perceived direction, a response consistent with a defensive function of the antennae in these nonchelate decapods. Overall sensitivity is greatest for hydrodynamic stimuli, a result interpreted as being important for the detection of and defense against large predatory fish whose nearby movements would generate broad, directional, water-current pulses.

Introduction

The crustacean second antenna is a prominent sensory appendage among aquatic arthropods, often terminating in a long segmented flagellum. A variety of setae and sensilla are found both on the proximal segments and along the annuli of the flagellum. These structures are believed to convey mechanosensory as well as chemosensory information (Derby, 1982), as do similar hairlike structures located elsewhere on the cephalic and thoracic appendages. The antennae are also used to signal behavioral information, for example during aggression (Bovbjerg, 1956). A specialized "antenna waving" behavior has been described in crayfish (Rubenstein and Hazlett, 1974) and in the clawed lobster *Homarus* (Solon and Cobb, 1980). In the crayfish, antennal waving signals appeasement following agonistic encounters (Ameyaw-Akumfi, 1979) and, although clearly functioning as a visual stimulus, also transmits tactile information (Bruski and Dunham, 1990). In *Homarus* the antennal flagellum contacts the claws of conspecifics and is perceived as a mechanosensory stimulus.

In the spiny lobster the antennae assume additional functions in defense, activities performed by the chelipeds in most other decapods. The Caribbean spiny lob-

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ster *Panulirus argus* uses the antennae additionally to make contact with other lobsters in the formation of migratory queues (Herrnkind, 1969). Unlike those of other crustaceans, the antennal flagellum in the spiny lobster is a robust appendage, well armed with forward-projecting spines similar to those on the carapace and other appendages. Pointed toward a potential predator, the antennae constitute a formidable defensive perimeter, particularly when many animals occupy a den, as is common in *P. argus* (Kanciruk, 1980). In fact, the antennae are used actively to fend off predators by directing the flagella toward the predator. If contact is made they push vigorously with the flagella to prevent further approach. If grasped or twisted, the antennal flagellum is often autotomized and a new, well-formed flagellum is regenerated at the next molt. The flagella are also brandished vigorously during agonistic encounters between conspecifics (Atema and Cobb, 1980).

For the spiny lobster, vision is clearly an important sensory modality for coordinating defensive antennal movements. Casual observation in the field or laboratory notes that the antennae respond readily to motion, even when the objects are moving above the water surface and therefore providing no mechanical cues. For example, animals in a laboratory tank typically rotate their antennae backward over their carapace in response to overhead movements. Slight changes in background illumination, even under dim light, cause lobsters to elevate their antennae to a more "alert" position. However, lobsters and other animals must rely increasingly on nonvisual sensory input during the nighttime hours, a period when lobsters are most active. Accordingly, the present study was initiated to test the antennal behavior of lobsters to nonvisual mechanosensory signals.

Mechanosensitivity in the spiny lobster antenna has been the subject of numerous studies (Laverack, 1964; Hartman and Austin, 1972; Tazaki and Ohnishi, 1974; Vedel and Clarac, 1976; Vedel, 1985), as has the reflex control of the antenna based on both local and distributed (leg) proprioceptive feedback (Schöne *et al.*, 1976; Vedel, 1980; Neil *et al.*, 1982). However, there has been no systematic investigation of antennal behavior in response to mechanosensory stimulation in the spiny lobster. In contrast, crayfish antennal behavior has been examined under a variety of conditions, *e.g.*, in response to controlled experimental stimuli such as water vibrations and water jets (Tautz, 1987; Schmitz, 1992), to natural hydrodynamic stimuli produced by small fish (Breithaupt *et al.*, 1995), and to tactile stimulation of the animal (Sandeman and Wilkens, 1983; Tautz, 1987; Sandeman, 1989). Antennal behaviors in the crayfish range from exploratory to stimulus tracking, and their role in prey localization has now been established (Sandeman and Varju, 1988; Zeil *et al.*, 1985; Breithaupt *et al.*, 1995).

In the present study we examine antennal behavior in the spiny lobster *Panulirus argus* in response to tactile and hydrodynamic (water jet) stimulation under controlled laboratory conditions. In addition, we observed the behavior of free-ranging lobsters in the field in response to the same type stimuli. Touch and sudden, localized water currents are stimuli representative of the environmental signals naturally encountered by lobsters while foraging at night in the open environment—for example, those produced by sharks, sea turtles, other large predatory fish—and by structural components of the environment including macroalgae, sea grasses, gorgonians, etc. Previous studies have demonstrated that lobsters utilize the hydrodynamic signals associated with waves and currents for orientation and locomotory behaviors (Walton and Herrnkind, 1977; Nevitt *et al.*, 1995). In the following experiments, we address the question of nonvisual mechanosensitivity and whether this type of information alone is effective in coordinating antennal movements in defensive behaviors. Our results indicate that lobsters direct their antennae toward the source or location of the stimulus, and that they distinguish directional signals from the front, from behind, or from alongside the animal.

Materials and Methods

Laboratory studies

Observations and experiments were conducted on juvenile spiny lobsters collected in the Florida Keys and shipped to the Florida State University Marine Laboratory, Turkey Point, Florida, and to the University of Missouri—St. Louis. The animals ranged in size from 12 to 19 mm carapace length and were housed either in unfiltered running seawater or artificial seawater and were fed cut squid and shrimp. Experimental results were based on responses from eight animals. Lobsters were individually marked for identification.

Antennal responses were recorded from animals tethered in the center of a 30 × 30 × 7 cm chamber filled with fresh seawater. To achieve near-normal posture and freedom of movement of the appendages during the experiment, a flexible, lightweight tether (1-kg test weight fishing line) was attached ventrally to the triangular sternum at the base of the legs and threaded through a small pivot hole in the bottom of the chamber. The tether allowed the animals freedom to turn and walk in place on the slick Plexiglas surface of the chamber floor. The chamber was centered on a turntable and rotated by hand.

The mechanosensory receptors of the lobster were stimulated by touch and by brief water-current pulses. For tactile stimulation a thin nylon filament (0.2 mm diameter, 7 cm long) attached to a thin wooden stick was manipulated by hand to lightly stroke the surface of the animal. This type of stimulus characteristically triggered ipsilateral antennal movements, although in some cases overt behaviors were not observed. Preliminary tests using a No. 4 camel-hair brush induced more pronounced responses including bilateral antennal movements, turning, and locomotion. The filament-stimulus technique was adopted because the resulting threshold responses were more site specific. Also, with the larger brush it was difficult to localize the stimulus when small animals were used or to rule out stimulation by near-field water currents prior to contact. Tactile stimuli were delivered randomly at different locations at 2-min intervals by drawing the tip of the filament in a single stroke over the following receptive fields (Fig. 1): lateral margin of the antennular flagellum (antennule), medial and lateral margins of the antennal flagellum (*i.e.*, front and back edges of the second antenna as seen in the resting posture; antenna med, antenna lat), lateral surface of the carapace (carapace), dorsal surface of the fourth leg (walking leg), lateral margins of the abdominal tergites (abdomen), and dorsal surface of the endopod and exopod (tailfan). These experiments were conducted in dim light and with the eyes of the lobster coated with black acrylic paint to further reduce visual stimulation. Responses attributed to visual stimuli were observed only if the eyes were shadowed directly; the response was presumably due to changes in light intensity but not movement *per se*. The paint was usually cleaned off overnight by the lobster using its pereopod tips.

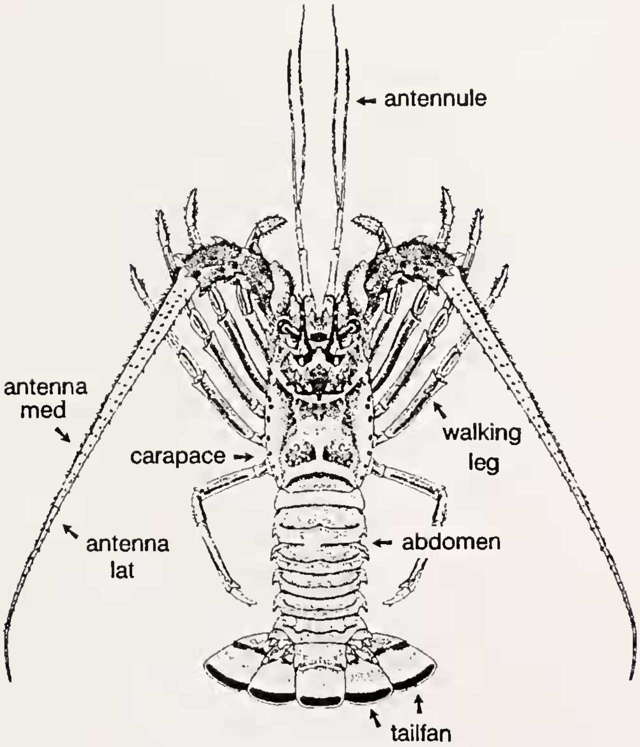

Figure 1. The spiny lobster *Panulirus argus* showing locations of tactile stimuli: antennule, medial antenna, lateral antenna, carapace, walking leg, abdomen, tailfan (endopod and exopod). Drawing of lobster adapted with permission from Sterrer (1986), Fig. 108.

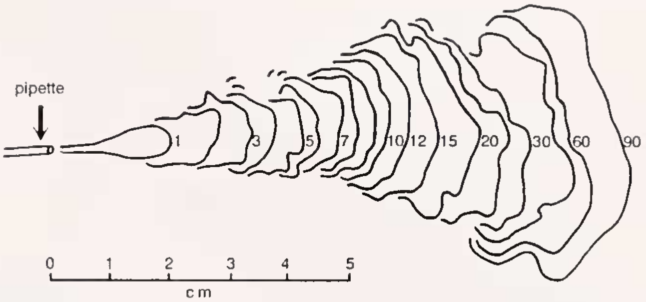

Figure 2. Laboratory water-jet stimulus visualized by addition of dye to the seawater-filled pipette. Numbered traces are video frames (30^{-1} s) and illustrate a water-jet stimulus pulse over a 3-s interval.

Water-current stimulation was produced by jets of water delivered from the tip of a disposable pipette directed toward the center of the test chamber. The pipette tip was positioned 5 cm from the center of the chamber and 2.5 cm above the chamber floor and was pointed downward at an angle 15° from horizontal. Preliminary tests showed this to be the most effective position on the basis of the strength of the stimulus jet and the size of the animals. A constant water-jet stimulus was delivered by depressing the rubber bulb of the pipette with an electromechanical transducer (Pasco Vibrator, Model SF-9324). The transducer was driven by pulses from a function generator (Tektronix FG 501) fed through a power amplifier and triggered by a stimulator (Grass S5). The stimulus pulse was calibrated by single-frame analysis of videotaped test pulses produced with a dye-filled pipette (Fig. 2). Mean axial velocity of the stimulus pulse at 5 cm, the distance to the center of the chamber, was 11.7 cm/s ± 4.1 cm/s SD ($n = 7$). Stimulus intensity, therefore, is within the range (4–20 cm/s) of suprathreshold pulse intensities that reliably elicit antennal responses in crayfish (Schmitz, 1992), but somewhat higher than threshold values (0.1–6.7 cm/s) for crayfish turning and escape responses (Ebina and Wiese, 1984). Overlays of the test-pulse image reveal that most of the dorsal body surface, excepting about the distal half of the antennae, is enveloped by the water jet.

Stimuli were presented from various angles, depending on the position of the turntable, the animal's turning movements, or both, and were presented at intervals of at least 2 min followed by rotation of the chamber. Stimulus jets were delivered only when the lobster was stationary with its abdomen fully extended and with both

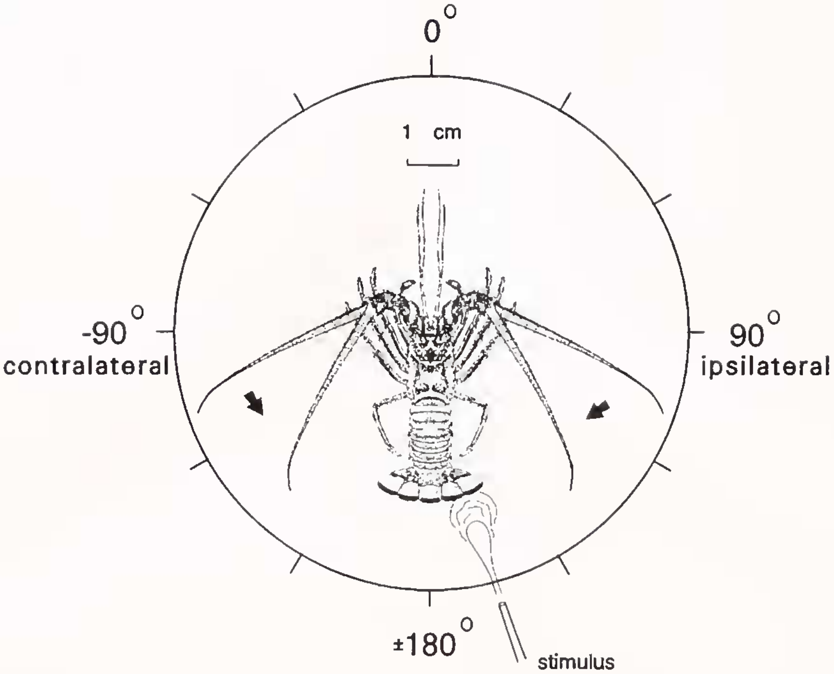

Figure 3. Stimulus and response angles for water-jet hydrodynamic stimulation. Stimulus angles are referenced to the middle of the carapace. A 0° stimulus is from in front of the lobster, ± 180° is from behind; positive values denote ipsilateral stimulation. A stimulus is illustrated at +165°. Angular antennal movements were measured with reference to the lobster's midline at the base of the antennal segments. Antennal end positions were subtracted from start positions so that sweeps of the left and right antenna (SLA, SRA) are denoted by negative values for backward rotation and positive values for forward rotation. Calibration scale corresponds to laboratory experiments with small animals.

antennae in the resting position, e., pointed laterally, more-or-less perpendicular to th dy axis. The water-jet experiments were conducted e dark using infra-red illumination (Sylvania, Mini) and an IR-sensitive CCTV camera (Baxall, CDG to monitor antennal responses. Antennal behavio recorded using a videocassette recorder (JVC Mod -378U) and measured directly from the video mon during playback. Rotation of the flagellum was mea d with reference to a point just anterior to the basal se ents of the antennae; stimulus angle was referenced the middle of the carapace (see Fig. 3).

Field studies

To complement the laboratory experiments, antennal responses were elicited from lobsters foraging or walking normally in their natural habitat. Our purpose was to determine whether lobsters exhibited similar responses to roughly analogous stimuli while in the open at night and vulnerable to predators. Observations were made while skin diving over areas of vegetated hard-bottom substrate at depths of 1–2 m near the Keys Marine Laboratory, Long Key, Florida. Animals whose carapace length was between about 50 and 70 mm were tested by stimulation devices scaled up to the larger juvenile and subadult-sized animals. For tactile stimulation a thin, flexible plastic rod (25 cm long, 3 mm in diameter) attached to a hand-held lobster "tickle stick" was used to stroke the animal. Water jets were delivered *via* a hand-operated kitchen baster extended by the addition of a 1-m length of PVC pipe (2.5-cm diameter O.D.). A thin plastic rod was attached to the tip so that when positioned above the middle of the animal it served as a gauge for presenting water jets at a constant distance. We confirmed that the jets made contact by observing the disturbance of fine sediment in front of the gauge. A small cloud of sediment was clearly visible below the stimulated lobsters.

Antennal behavior was tested as the lobsters foraged at night in the open so that the animal could be stroked or squirted by seawater at various sites or directions. On the nights of observation (23–26 June 1994), moonrise ranged from 1951–2219 h EDT, so natural moonlight was low or absent during the dive periods (~2100–2400 h). Observations were made using dive lights equipped with red filters (λ = 680 nm) to minimize visual disturbance of the animals. Previous experience indicated that lobsters are insensitive to red light, and under these conditions they continued foraging undisturbed. One diver presented the stimulus while a second diver recorded antennal responses. Diver training sessions were conducted to standardize presentation of stimuli and recording of antennal responses. Antennal positions were noted prior to the stimulus and marked on data sheets constructed on nontear paper (Avery #6725) predrawn with lobster silhouettes and 60° sectors of possible antennal rotation. After stimulus presentation, approximate final positions were noted along with stimulus location and direction and the estimated size of the lobster. Each animal was stimulated no more than twice, with lobsters selected as they were encountered. Only stationary lobsters were tested, as in the laboratory experiments; preliminary trials indicated that walking animals were less responsive and that accurate estimation of response angles was made more difficult.

Data analysis

The parameters for measuring stimulus and response angles are diagrammed in Figure 3. A water jet stimulus of 0° is from the front of the lobster and ± 180° is from behind; positive angles represent ipsilateral stimuli and negative angles contralateral. Start positions (resting) and end positions ranging from 0° to 180° and sweep angles (*i.e.*, start minus end positions such that backwards sweeps are negative in sign and *vice versa*) were evaluated for both antennae (see Fig. 3). As in a previous study in the crayfish *Procambarus clarkii* (Schmitz, 1992), responses of the left and right antenna did not differ significantly. Thus, data have been pooled and means and standard deviations, 95% confidence intervals, and circular means and angular deviations (Batschelet, 1981) are evaluated for the antennal responses. Significant differences are based on 95% confidence intervals. Circular means are not shown here because they do not differ by more than 2.4° (usually by about 0.1°) from the linear means.

Results

Antennal responses to hydrodynamic stimulation

Laboratory studies. Animals tethered in the experimental chamber were allowed to adapt for 30 min. Occasionally animals walked or tailflipped spontaneously during the experiments. However, tailflips were never elicited by mechanical stimuli. Quiescent lobsters frequently exhibited a slow metachronal stepping rhythm, an activity pattern observed in other decapods, and rested with the abdomen extended and the antennae pointing laterally at a mean angle of 90.5° (see Fig. 4, "+" symbols). For experimental purposes, stimuli were delivered only when the antennae pointed laterally. In walking animals the abdomen was also extended, but antennal positions were somewhat more varied and occasionally the flagellum was actively swept forward and backward.

Whether quiescent or walking, animals generally held the antennal flagellum at an upward angle of about 10°–15°. Infrequently, the antennae were raised higher, as estimated by the shadow cast from the IR source. The more horizontal antennal posture differs from that of quiescent animals in lighted holding tanks; under those conditions the flagellum often points vertically. A vertical antennal position may be more characteristic of unrestrained animals that always seek a corner of the tank or natural structure with vertical relief, *e.g.*, a sponge; during experiments, animals were tethered in an open unstructured environment. The antennal posture of larger lobsters encountered while they are actively foraging is similar to that observed in the tethered animals. Unless disturbed, the antennae point laterally, whether the animal is walking or stationary during feeding, and the abdomen is always extended.

Water jets delivered to small tethered lobsters elicit a bilateral antennal response in which the flagella are swept forward or backward depending on the stimulus direction. No antennal response was observed in 12% of the stimulus trials (n = 30 of 252). Initial movement is rapid and occurs within 0.5–1.0 s; a secondary movement of the flagellum may follow at a slower rate. The initial, more consistent antennal response is presented in this study and is further distinguished from antennal movements associated with startle responses involving locomotion. Antennal start and end positions (mean and 95% confidence intervals from eight experiments) relative to the stimulus angle are illustrated in Figure 4. Mean start positions for different stimulus angles range between 82.9° and 99.5° and average 90.5° ± 18.5° SD, perpendicular to the rostrocaudal axis. Mean end positions reflect a general rotation of both antennae toward the stimulus, *i.e.*, sweeps in a rostral direction for frontal stimulation (0°–60°) and caudally for lateral or caudal stimulus angles (>60° to 180°; Fig. 4). Significant differences between antennal start and end positions for a given stimulus angle class are found only with caudal stimulation (>150°–180°) as indicated at ±165°.

Thus, tethered juvenile spiny lobsters show bilateral antennal sweeps that are directed forward for frontal hydrodynamic stimuli and backward for all remaining stimulus directions. Sweep angles irrespective of antennal position are illustrated in Figure 5 as means for the 30°-stimulus angle classes. Significant differences demonstrate that antennal responses reflect the stimulus direction in the broad categories of frontal (0°–60°), lateral (>60°–150°), and caudal (>150°–180°): that is, backward sweeps are significantly greater for caudal *versus* lateral stimulation, and frontal stimuli produce forward sweeps

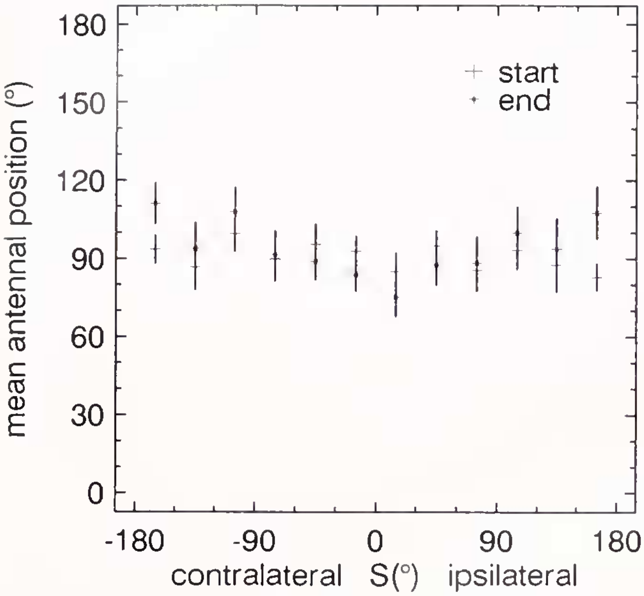

Figure 4. Antennal positions of small, juvenile spiny lobsters in laboratory experiments along with responses to ipsilateral (positive *S*-values) and contralateral (negative *S*-values) water-jet stimuli. Mean start (+) and end (*) positions are shown along with 95% confidence intervals ($n = 15$–29) for individual 30° stimulus categories; categories are represented graphically at their midpoints, *e.g.*, 15° for 0°–30° stimulus angles. See Figure 3 for illustration of measurement parameters.

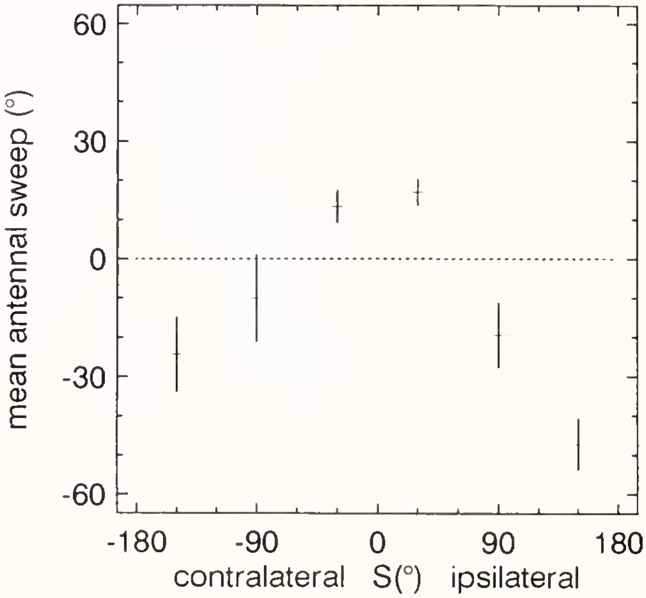

Figure 6. Dependence of antennal sweeps of foraging juvenile and subadult-sized spiny lobsters on the direction of a water-jet stimulus. Mean sweep amplitudes with 95% confidence intervals ($n = 7$ up to 33) are shown for 60° stimulus angle classes. Data are results of field experiments and compare with laboratory results in Figure 5.

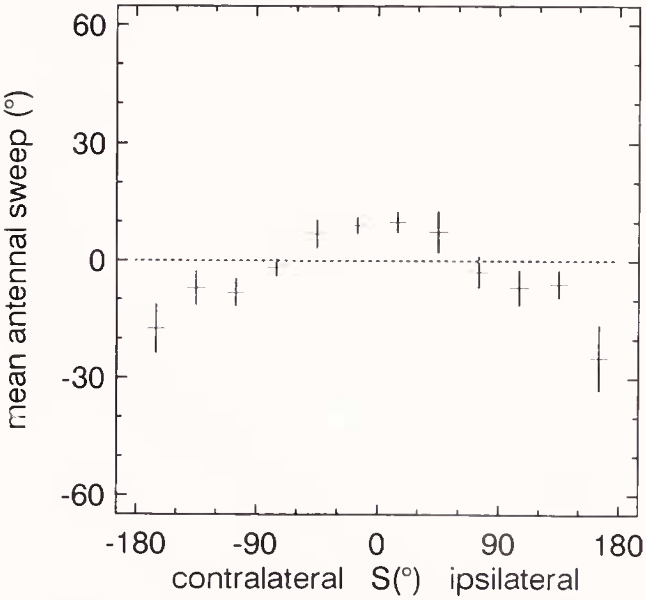

Figure 5. Dependence of antennal sweeps on the direction of water-jet stimuli in laboratory experiments with juvenile spiny lobsters. Responses are illustrated as means of antennal sweep amplitude with 95% confidence intervals for 30° stimulus angle classes. The antennal sweep data are based on the start and end positions shown in Figure 4.

that differ significantly from those of other directions. These results indicate that spiny lobsters not only distinguish between frontal and caudal stimuli, but also are able to more accurately localize the stimulus. However, responses for corresponding stimulus angles on the ipsilateral and contralateral side of the animal are not significantly different (Fig. 5), and indicate that the mean antennal response is statistically symmetrical. Although not significantly different, the mean ipsilateral response to caudal stimulation is greater by 7° and is consistant with a much greater ipsilateral response observed in the field studies (see below).

Field studies. Observations of 119 antennal responses were recorded in juvenile and subadult-sized spiny lobsters in their natural habitat, with lobsters receiving either one or two stimuli. Despite inherent variation in the strength of the hand-delivered stimuli, the lobsters responded in a consistently patterned way. Mean antennal sweeps in response to water jets are shown in Figure 6 and correspond closely to those analyzed in the laboratory (*cf.* Fig. 5). Again, frontal stimulation (0°–60°) produces bilateral forward sweeps, whereas both antennae sweep backward for stimulus directions greater than 60°. Response amplitudes also increase as the stimulus shifts caudally. For stimuli in the caudal sector (150° stimulus-angle class) lobsters are able to lateralize, *i.e.*, to differentiate between water jets from the right and left side, as indicated by significantly greater antennal sweeps of the ipsilateral antenna. Overall, sweeps from larger untethered animals in the field, especially those of the ipsilateral antenna, show nearly twice the amplitude of those from smaller tethered lobsters in laboratory experiments. The number of no-response trials was low (5%; 6 of 119).

Behavioral observations in the field revealed features of the lobster's response to hydrodynamic stimuli that were not observed in tethered animals. After the antennal response, lobsters frequently reacted without further stimulation–either turning toward the stimulus and then tailflipping away or tailflipping immediately (Table I). In approximately one-third of the stimulus trials involving lateral or caudal stimuli, lobsters turned toward the stimulus; frontal stimuli did not elicit turning. Turn angles were not measured, but in most instances the lobster rotated its body axis to face the approximate stimulus direction. The turning response, and its absence for frontal stimulation, is further indication of the lateralization in sensitivity to off-axis hydrodynamic stimuli. Tailflips occurred to a varying degree for all stimulus directions, but again at higher frequencies for more caudal directions. The escape response occurred both independent of (n = 16) and subsequent to (n = 19) the turning response.

Antennal responses to tactile stimuli

Laboratory studies. The antennal response elicited in small lobsters by touching the antennule, the medial or lateral edge of the second antenna, the carapace, a walking leg, the abdomen, or the tailfan is illustrated in Figure 7. The light strokes from a flexible nylon filament appear to be near threshold because responses were elicited only from the ipsilateral antenna; no response was observed in nearly one-third of the trials (31 of 108). The antenna is swept forward when contact is made with the antennule or the medial edge of the long antennal flagellum, although no response was observed in nearly half of the tests (45%, 10 of 22). All the remaining tactile stimuli elicit backward sweeps, and with a greater response frequency (76%); out of 86 total tests only a single forward sweep was observed. Thus, small lobsters move their long antennae toward the location of a tactile stimulus and accurately distinguish tactile sensory input from anterior and posterior body regions. Lateralization of stimulus sensitivity was absolute; only the ipsilateral antenna responded to stimulation either of the appendages or of the lateral surface of the carapace and abdomen. The distinction between rostral and caudal was especially pronounced for antennal stimulation—responses were significantly different and resulted in forward and backward sweeps when the stimulus was applied respectively to the medial and lateral edge of the flagellum. Overall, forward and backward responses differed significantly. However, within the categories of tactile stimuli that produce forward and backward responses, sweep amplitude is not significantly different (see Fig. 7).

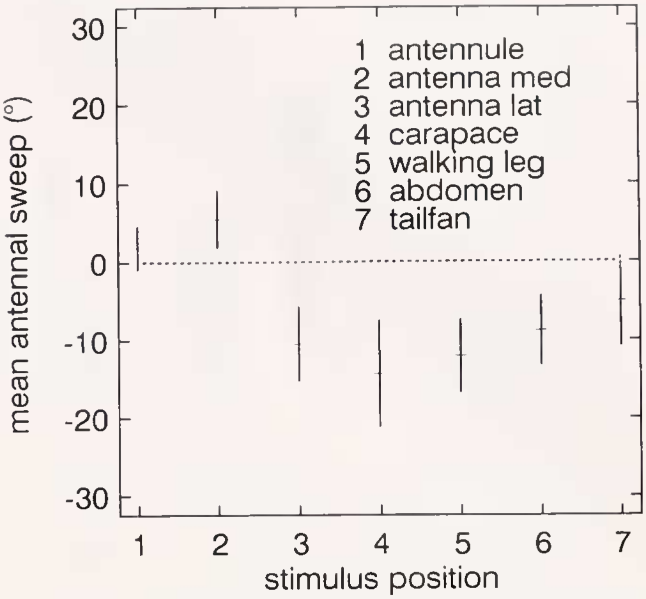

Figure 7. Dependence of sweeps of the ipsilateral antenna on the location of tactile stimuli in laboratory experiments with small juvenile spiny lobsters. Mean sweep amplitudes and 95% confidence intervals (n = 7 up to 20) are shown; stimulus locations are indicated in the inserted legend.

Table I

Turning and tailflip escape behaviors of foraging spiny lobsters in response to hydrodynamic water-jet stimuli

Stimulus sector	0°–60°	>60°–120°	>120°–180°
Turns (%)	0	36*	37
Tailflips (%)	14	31	54
Number of trials (n)	37	36	35

With one exception (*), all turns were ipsilateral or toward the direction of the stimulus.

Field studies. In their natural environment, juvenile and subadult-size lobsters responded to tactile stimuli (Fig. 8) in similar fashion to the smaller animals tested in the laboratory (*cf.* Fig. 7), except that responses were frequently bilateral, involving simultaneous sweeps of both antennae in more than two-thirds of the stimulus trials. The tactile stimulus applied under field conditions undoubtedly was more variable and presumably involved higher suprathreshold strengths. Due to the difficulty of observing both antennae and recording accurate response angles without aid of video playback, responses are not quantified by amplitude of antennal sweep. However, antennal responses in field-tested lobsters generally involved large sweeps (>30°), and the an-

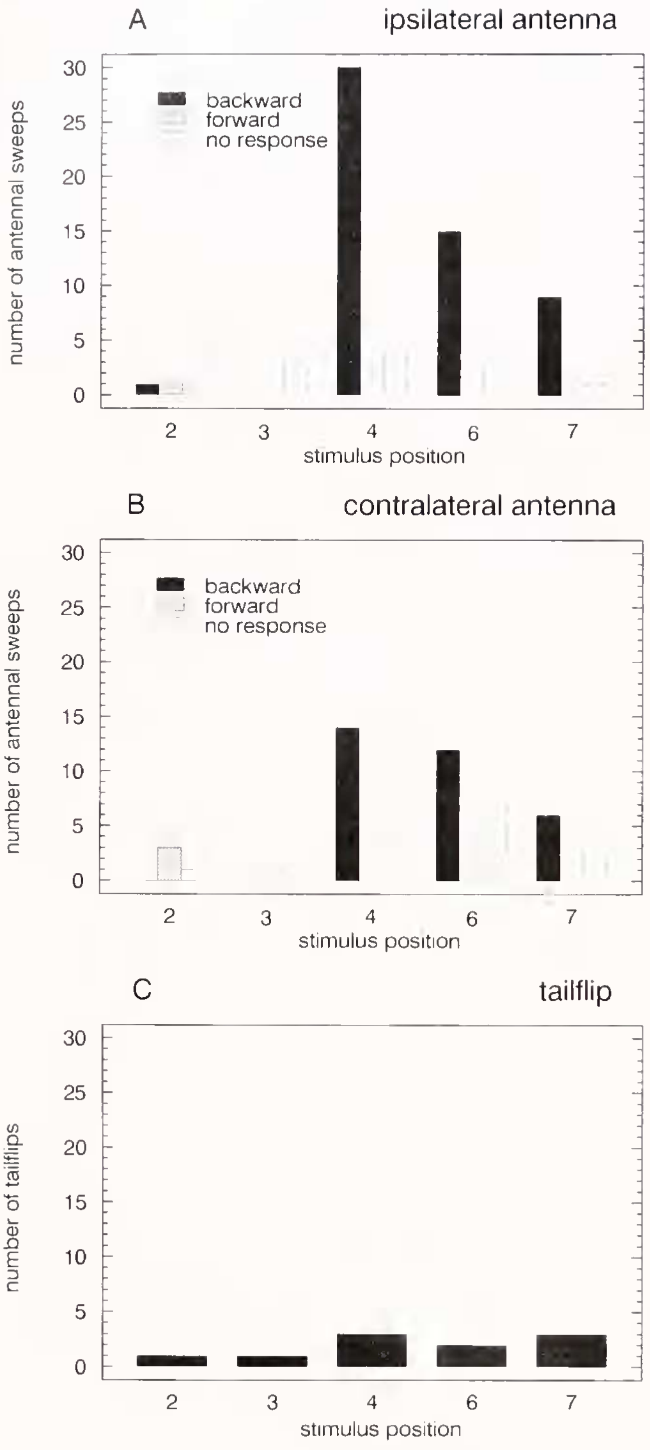

Figure 8. Antennal response frequencies to tactile stimulation in juvenile and subadult-sized spiny lobsters in field experiments. Ipsilateral (A) and contralateral (B) antennal responses are illustrated separately for the following stimulus locations: 2—antenna medial, 3—antenna lateral, 4—carapace, 6—abdomen, 7—tailfan, as in Figure 7. Bars represent backward sweeps (filled), forward sweeps (hatched), and no response (unfilled) of the antenna in both A and B. Tailflips elicited by corresponding tactile stimuli are illustrated in C.

tenna frequently crossed over the midline of the animal. In correspondence with the laboratory data, the ipsilateral antenna is swept backward when the lateral surface of either the carapace or abdomen, or the dorsal surface of the tailfan uropods, is touched (Fig. 8A); response failures were low (11%, 8 of 72). Similarly, the contralateral antenna responds vigorously with backward sweeps in response to carapace, abdomen, and tailfan stimulation (Fig. 8B), although the failure rate was higher (39%, 24 of 61). Forward sweeps of the antennae were never observed for thoracic or abdominal stimulation. Forward sweeps were elicited, however, by touching the medial edge of either antenna (stimulus position 2, Fig. 8A, B). Foraging lobsters did not respond to the few stimuli applied to the lateral edge of the antenna (stimulus position 3, Fig. 8A, B). Antennule and leg stimulation was omitted due to the uncertainty of localizing the stimulus to these appendages under field conditions. In addition to antennal movements, tailflipping behavior was elicited by tactile stimulation in field experiments, with tailflips occurring more often when more caudal surfaces of the animal were touched (Fig. 8C). Tailflip backward swimming rapidly steered the lobster away from the stimulus irrespective of the stimulus site.

Discussion

Mechanosensory-induced antennal behavior in the spiny lobster

We have analyzed the behavior of the spiny lobster *Panulirus argus* in response to hydrodynamic and tactile stimuli. Quantitative laboratory studies on small juvenile lobsters and semiquantitative field analyses on larger animals under natural field conditions were designed to demonstrate mechanosensory functions independent of the visual system. The primary behavioral response is an immediate sweep of the antennal flagella in the direction of the stimulus. Laboratory and field results are consistent with regard to the antennal response, but related aspects of the behavior differ somewhat. For example, antennal movements were the sole overt response in laboratory experiments in which the strength of both water jet and tactile stimuli was closer to threshold and carefully controlled. Under field conditions the antennal response was followed in many instances by a more vigorous response in which the lobster turned to face the direction of the water jet, gave a tailflip escape response, or both. Field water jets also produced higher overall response percentages, *i.e.*, 95% *versus* 88% for laboratory water jets.

Behavioral variability may result from factors such as the size difference of the animals used in the laboratory and field studies. Although larger animals respond with more vigorous turn or escape responses, this is not predicted by the developmental differences displayed in the clawed lobster *Homarus* where escape responses in small animals give way to defensive displays in larger animals (Lang *et al.*, 1977). However, the ontogeny of defensive behavior in *Homarus* is associated with an allometric increase in claw size. The spiny lobster has no chelae. Alternatively, the absence of escape responses under laboratory conditions may be at least partly a result of restraint-induced inhibition of escape behavior, as demonstrated previously in the crayfish (Krasne and Wine, 1975). Even though restraint in our laboratory experiments allowed simulated walking, animals nonetheless experience less freedom of movement than foraging animals. In addition, turns and tailflips may be due in part to a more suprathreshold level of stimulation associated with hand-delivered stimuli in the field.

Mechanosensory-induced antennal responses, along with turns and tailflips, indicate the ability of spiny lobsters to localize (within 30°) the source of hydrodynamic signals, and to respond selectively to direct contact with their body surface. Water jets, regardless of direction or intensity, trigger bilateral antennal movements. The bilateral hydrodynamic response characteristically involves same-direction movement of both antennae, with the contralateral antennal response statistically indistinguishable from that of the ipsilateral antenna (Fig. 5). In effect, both antennae sweep toward a stimulus directed from the front or rear of the animal. The ipsilateral antenna also moves toward a lateral stimulus but the contralateral response is seemingly anomalous, essentially pointing in the opposite direction. Nevertheless, the bilateral antennal response reflects activation by the hydrodynamic stimulus of a receptive field encompassing both sides of the animal, in comparison to the more localized tactile stimulus, and suggests that there is strong bilateral coupling of direction-specific neural elements underlying the antennal behavior.

On the other hand, threshold-level touch elicits exclusively ipsilateral antennal movements (Fig. 7). The unilateral response to a more localized tactile stimulus indicates that antennal motor circuits also exhibit independent, uncoupled control of the appendage. For responses to light touch, stimulus lateralization is absolute. In foraging, unrestrained animals, however, tactile stimulation again elicits a bilateral response in which both antennae sweep the same direction. As with hydrodynamic stimulation, field stimuli are apparently suprathreshold and trigger tailflips along with antennal responses (Fig. 8).

The direction and degree of antennal sweep responses are nonetheless clearly related to stimulus direction or location and direct the antennae toward the stimulus. Water jets from in front of the animal, broadly defined by a ± 60° arc, trigger almost exclusively forward sweeps of the antennae (Fig. 5), and these differ significantly from backward movements for all other stimulus directions (Figs. 5 and 6).

Tactile responses also broadly distinguish between anterior and posterior stimulus sites. Contact with the antennules or the medial edge of the antennal flagellum produces forward rotation; all other sites trigger backward rotation. As with hydrodynamic stimuli light touches trigger a relatively weak response, with a maximum mean amplitude of $-14°$ for carapace stimulation (Fig. 7). Except for direction, stimulus site has little effect; that is, response amplitude does not vary significantly according to the relative anterior-to-posterior location of the stimulus, at least for light contact. However, the distinction between an anterior and posterior tactile stimulus is particularly clear at the level of the antenna, where medial and lateral sites trigger responses of opposite direction. The antennal stimuli used here may activate proprioceptive resistance reflexes (*cf.* Vedel, 1980) in addition to responses mediated by tactile receptors; responses mediated by thoracic and abdominal inputs would originate primarily from tactile and hydrodynamic receptors.

Comparisons of antennal responses in palinurid and astacid decapods

The behavior of the antennal flagellum in the spiny lobster *P. argus* is different in a number of respects from that in the chelate decapod crustaceans. In this study, where lobsters were observed in both active and inactive states, the antennae were held in a lateral resting posture perpendicular to the long body axis. Resting position may vary with circumstance: for example, in small lobsters (<20 mm carapace length in our studies) the flagella are often held vertically, and the animals themselves are less likely to occupy flat, horizontal benthic substrates. In crayfish, as with *P. argus*, the resting antennal position is also near horizontal, but the flagella point in a more rostral to rostrolateral direction, *e.g.*, 20°–60° in *Orconectes limosus* (Tautz, 1987), 20°–50° in *Cherax destructor* (Zeil *et al.*, 1985), and 50° in *Procambarus clarkii* (Schmitz, 1992). The lobster *Homarus americanus* is exceptional in that the antennae at rest are held fully flexed backward alongside the cephalothorax (Sigvardt, 1977). The backward position in *Homarus* correlates with the prominent chelipeds, which not only present a defensive barrier but also contain many mechanosensory receptors (Derby, 1982). In crayfish, the forward resting position presumably emphasizes the mechanosensory function of the antennae, whereas in the spiny lobster a more lateral position may be optimal for combined sensory and defensive functions.

Antennal responses to hydrodynamic stimuli in crayfish are in general similar to the bilateral responses reported here for the spiny lobster, although some differences have been noted. Surface vibrations from a dipole oscillator positioned laterally elicit bilateral antennal movements in *O. limosus* (Tautz, 1987), but the antennae respond independently, the ipsilateral antenna moving toward the stimulus while the contralateral antenna moves in either direction. A dipole oscillation is a more complex stimulus (Wilkens and Douglass, 1994) and may account for the variable response of the contralateral antenna. Schmitz (1992) employed water jets to stimulate primarily the abdominal region in *P. clarkii* and, as in *P. argus*, a bilateral, same-direction response was elicited. However, with jets centered on the tailfan and limited primarily to lateral and caudal sectors (equivalent to those defined in the present study), only backward responses were observed. The antennal movements in *P. clarkii* also demonstrate lateralized sensitivity for particular stimulus directions—rostrolateral when using stronger water-jet currents, and lateral to caudolateral for weaker stimuli. By reversibly blocking hydrodynamic receptors on the tailfan, Schmitz (1992) also demonstrated the importance of tailfan mechanoreceptors for more cephalic reflex behaviors. Lateralization was clearly evident in *P. argus* for the most caudal stimulus directions but, because our stimuli were centered on the mid-thorax region, the receptive fields affected were somewhat different. As in crayfish, however, in our spiny lobster, the tailfan played a prominent role as a sensory system in that antennal responses were largest and showed significant lateralization when the stimulus was aimed at the tailfan, *i.e.*, in the caudal sector.

Among crayfish and lobsters, responses to tactile stimuli show greater variability than to hydrodynamic stimuli, and the adaptive significance is not always clear. As reported here, the spiny lobster moves one (ipsilateral) or both of its antennae backward for most stimulus sites, the exceptions being the antennules and the medial edges of the antennae. In two Australian crayfish, *Euastacus armatus* (Sandeman and Wilkens, 1983) and *C. destructor* (Sandeman, 1985), however, tactile stimulation of the branchiostegite (carapace) elicits strong, forward extensions of the ipsilateral antenna. Cephalic (tegumentary receptive fields) stimuli sometimes produce backward sweeps in *Euastacus*. Touching or pinching the telson and uropods of these crayfish, as with *P. argus*, triggers flexion of the flagellum in an apparent rotation of the appendage toward the site of potentially threatening contact. The response is similar for *O. limosus* but, as for dipole stimulation, the contralateral antenna moves variably in either direction (Tautz, 1987).

Rostral tactile stimulation also yields different responses. In the spiny lobster, a tactile stimulus "in front" of the animal triggers a forward, reflex extension of the ipsilateral antenna. In the chelate astacids the response is opposite. In *Cherax* the antenna withdraws (flexes) when touched (Sandeman and Varju, 1988), and in *Homarus* disturbances in front of the animal cause the antennae to assume the "resting," backward-pointing position (Sigvardt, 1977). Touching the rostrum in *Orconectes* has a mixed effect (Tautz, 1987). Backward sweeping of the flagellum in crayfish is apparently associated with, and precedes, aggressive behavior. For example, touching the tip of the antennae in *Cherax* triggers withdrawal of the antennae, after which the crayfish turns, moves forward, and grasps with the chelae (Zeil *et al.*, 1985; Sandeman and Varju, 1988).

Natural history of antennal behavior

The functional anatomy of the spiny lobster antennae suggests strongly that they assume a defensive role not shared by the antennae of chelate decapods. The behavioral responses described in the present study, in which movements in response to both hydrodynamic and tactile stimuli are toward the source of the stimulus signal, support this observation. It is not known if pointing the flagellum toward the stimulus enhances mechanosensitivity, as is postulated for the crayfish (Tautz, 1987), but the benefit of aiming the stiff, spiny flagellum at a potential predator is clear. The mechanosensory response is essentially equivalent to visually mediated movements of the antennae, although the latter have not been quantified, and therefore would be synergistic with or act in lieu of visual guidance in the dark.

The natural history of spiny lobsters suggests several functional interpretations for the observed antennal responses, especially for animals on open substrate at night. The primary nocturnal predators of juvenile lobsters are fish (*e.g.*, snappers, grouper) and sharks (*e.g.*, bonnet head and nurse sharks) (Smith and Herrnkind, 1992). These large, actively swimming predators are likely to be detected first by water pulses (*e.g.*, as measured by Bleckmann *et al.*, 1991), not unlike our water jets, caused by water turbulence as they pass close by or, especially, turn and circle the potential prey. The high response rate (95 percent) to water jets and the nature of the response—frequent tailflipping and rapid turning toward the jet's source (Table I)—indicate an active escape response or preparation for defense. By both directing the antennae and turning the body toward the stimulus, a lobster presents its best-armored body regions (rostral horns and spine-studded antennal bases) and its fencing weapons (antennal flagella) to the potential attacker. Simultaneously, the far more vulnerable abdomen is better protected and readied for propulsion away from the attack. This also may explain the higher responsiveness to the more posterior water jets and tactile stimuli; these induced the largest bilateral antennal sweeps and the most tailflipping. Bringing both antennae to the stimulated region seems the best tactic to detect and ward off a predator whose next direction of approach cannot be readily predicted.

Responses to tactile stimulation in the field were less frequent and less pronounced than responses to hydrodynamic stimuli, particularly in the anterior body region. This probably resulted in part from the lightness of the stroke we applied, but otherwise represents the normal response of lobsters we observed being brushed by seagrass blades, sea whips, and other common objects moved by water currents as lobsters forage and move about. In contrast, a large fish is less likely to brush against only a small body area. However, a strong hydrodynamic stimulus almost certainly signifies a large swimming animal, many of which are potential predators, as discussed above.

In this study we did not examine other potential antennal functions or responses. The antennae are not known to be involved in feeding; antennaless individuals forage normally using the antennules and pereopods (pers. obs., W.F. Herrnkind). They may have a limited role in social communication (Lipcius *et al.*, 1983), and their position is regulated during locomotion depending on walking speed (Bill and Herrnkind, 1976). That is, while slowly walking and foraging, they are held more-or-less perpendicular to the body or slightly forward. As speed increases, both antennae are swept further forward, thus decreasing hydrodynamic drag, as often seen in mass queuing of migrating lobsters (Bill and Herrnkind, 1976). How other stimuli influence antennal responses in such situations is not yet known. The high level of responsiveness and clear patterns from our field study of free-moving lobsters invites further research. In particular, measurements of hydrodynamic features of moving lobster predators modeled by more controllable devices might give insight into both the physiological processes and the events to which they are tuned evolutionarily.

By contrast, in crayfish and *Homarus* the antennae are involved in the behaviors of communication, *e.g.*, antennal whipping among conspecifics (Rubenstein and Hazlett, 1974; Solon and Cobb, 1980), exploratory activities (Sandeman and Varju, 1988; Zeil *et al.*, 1985), and agonistic and feeding behaviors (reviewed by Voigt and Atema, 1992). The active role played by the crayfish antennae in prey localization has been shown recently using natural stimuli from live fish (Breithaupt *et al.*, 1995). In these experiments, reversibly blinded crayfish (*P. clarkii*) react to hydrodynamic disturbances produced by small swimming fish with accurate body turns and cheliped movements that result occasionally in prey capture. The orientation responses are always preceded by antennal sweeps, with both antennae moving toward the stimulus. In contrast to the spiny lobsters analyzed here using artificial stimuli, the ipsilateral antennal movements of the crayfish are usually directed backward whereas those of the contralateral antenna are smaller and directed forward, often resulting in antennal contact with the fish. We do not know yet whether spiny lobsters facing a live fish (be it predator or prey) respond in a similar way. In these nonchelate decapods, however, moving the well-armed antenna toward the stimulus source would be an excellent way to gain more information about the location and size and nature of a potential predator, as well as to present a defensive front.

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